

At a still later period the nerve given off from the ganglion unites with the anterior nerve-root.

The development of the anterior nerve-roots is far simpler than that of the posterior.

Some little time after the appearance of the posterior roots there spring, on each side, from the ventral corner of the spinal cord, a series of conical outgrowths. These correspond in number with the muscle-plates, and are the rudiments of the anterior roots of the spinal nerves.

These outgrowths are not vertically below the posterior roots, a feature which remains permanent in the adult.

The points of attachment of the anterior roots undergo no change of position like those of the posterior roots; and after they have attained a considerable size they unite with the latter.

The author has also observed that the posterior roots of some and probably of all the cranial nerves develop in the same way as the posterior roots of the spinal nerves, and points out the bearing of this upon the morphological relations between the spinal and cranial nerves.

The remainder of the paper consists of a series of speculations upon the bearing of the above-mentioned facts upon various physiological and morphological problems. These, for the most part, do not admit of being abstracted.

One point the author mentions is the probable homology of the commissure he has detected uniting the dorsal ends of the posterior nerve-roots with the commissure he has described in a previous paper ("A preliminary Account of the Development of the Elasmobranch Fishes," *Quart. Journ. of Micros. Science*, October 1874, plate 15. fig. 14), which at first unites all the branches of the vagus nerve, and which is subsequently represented by their common junction before uniting with the medulla oblongata.

## II. "On the Structure and Development of the Skull in the Batrachia."—Part II. By W. K. PARKER, F.R.S. Received October 28, 1875.

(Abstract.)

In the present communication I wish to correct, as much as possible, what now seems to be erroneous in my former account of the Batrachian skull (that of the frog, *Phil. Trans.* 1871), and also to describe and illustrate the stages in the skulls of three kinds of toads.

Happily for me, Professor Huxley took up this subject at the beginning of last year; and I had frequent opportunities of working, as well as for discussion, with him.

It was soon made plain to me that in my former account of the behaviour of the visceral arches I had been wrong in describing the hyoid arch of the *third stage* as composed of an upper and a lower piece.

The supposed upper piece was merely the outer edge of the arch in front, the mandibular arch; and therefore all reasonings upon the metamorphosis, afterwards, of such a coalesced segment fall to the ground.

Professor Huxley showed me, and my new researches told the same tale, that the hyoid arch does not coalesce at all with the mandibular; that the "columella," whether answering to the "hyomandibular" of a fish or not, has no existence as cartilage, even in young frogs and toads that have taken to land life; afterwards, when they are one third larger, this cartilage appears.

Professor Huxley, and my own observations agree with his, also showed me that the *stapes* is not formed by the separation of a plate of already formed cartilage, but chondrifies later than the auditory sac and much earlier than the columella: in the Urodela it is formed by the segmenting off of a flap of the chondrified capsule. Our mutual researches, after these errors were made evident to me, gradually brought us into greater harmony in our interpretation; and the working out by Professor Huxley of *Menobranchus*, and by myself of others of the Urodela, has been of great service in making clear the meaning of the more complex skull of the Anura.

Being well provided with materials for working at the common toad's skull, and, through the kindness of friends\*, for various stages of the two "aglossal" toads, namely *Dactylethra* and *Pipa*, it came to pass that I was in a good position for searching out this subject further, with new light and new material.

Moreover these are not the only types of the Batrachia that have more recently engaged my attention; but the great bull-frog and the paradoxical frog have also had various stages of their skulls laboured at by me. These would have swelled my paper to too great a size; I hope to offer them when the tree-frogs, *Bombinator* toads, and other kinds have been studied.

In this paper I have given, first of all, correcter figures of the nasal labyrinth of the adult frog. Before my former paper was in print I had seen that in the bull-frog the "trabecular cornua" kept their distinctness on the front nasal wall. Professor Huxley has discovered *rhinal processes* in *Rana esculenta* and in *Rana temporaria*. He also showed me a distinct nucleus of cartilage in front of the nasal sac. There are *two* such cartilages on each side, as I soon found, the modified and subdivided "upper labials;" these are shown in the new figures.

By comparison of the skull of the Anura with that of the tailed Amphibia, a better idea can be had of the relations of the mandibular pier

\* I am indebted to Professor Huxley for adult skulls of *Dactylethra* and *Pipa*; to Dr. Dobson, F.L.S., of Netley, for another adult *Dactylethra*; to Mr. T. J. Moore, of the Liverpool Free Library and Museum, for four stages of the larval *Dactylethra*; to Dr. Günther, F.R.S., for embryos of *Pipa*; and to Professor W. H. Flower, F.R.S., for ripe young of the same.

with the auditory capsule: newer and more correct names of the attaching processes of the "suspensorium" are here given, in accordance with the nomenclature adopted by Professor Huxley in his memoir on *Menobranchus* (Proc. Zool. Soc. 1874, p. 186).

For instance, the band which connects the mandibular arch primarily with the trabecular is now called the "pedicle," and the secondary process which binds on the ear-sac is the "otic process." There is no "ascending process" over the orbito-nasal nerve, as in the salamandrian forms; and the apex of the pedicle losing its distinctness, its lower part forms a condyle which articulates with the outer face of the auditory mass below.

The apparent distinctness of this part in the young frog kept up the illusion as to its being a part borrowed from the next arch. It was called by me the "infra-hyomandibular."

The cartilage which I erroneously supposed to be the rudiment of the "columella" lies *over* the portio dura nerve; it was called by me the "supra-hyomandibular." It is in reality the rudiment of the cartilaginous *ear-ring*.

All this, thanks largely to my friend and fellow worker, is made plain now.

In frogs it is not quite easy to recognize the supero-anterior element of the *double* hyoid arch of osseous fishes in the columella; in toads it is easier.

In the frog a small cartilaginous segment is cut off from the proximal end of the shaft of the columella, and lies between it and the stapes. In toads the proximal element is the longer of the two, and is distinguished by being ossified separately, and not by subdivision of the cartilage.

Hence it is not a wild supposition that the proximal shaft-bone may be the "hyomandibular" and the distal the "symplectic," its unossified end being dilated as the "extrastapedial."

In osseous fishes we have this supero-anterior bar in the hyoid region ossified by two centres, but no stapes; in the Urodela the stapes, but, as a rule, no supero-anterior bar; in toads we have both, whilst in frogs the apex of the upper pier is a free nucleus of cartilage.

The primordial cartilaginous skull of the common toad is here worked out, the subjects being tadpoles only one third of an inch in length; their black colour and granular texture made them most difficult objects to interpret, and cost me much anxious labour.

Then in a series of stages comparable with those of the common frog I have traced the metamorphosis of the facial arches, so that the skull of the two common kinds of Batrachia will now be intelligible.

In the tadpole of *Dactylethra* there is much that is new and strange; there are neither suctorial mouth nor horny jaws. The upper labial forms the edge of a broad mouth with an *underhung* lower jaw, the head being extremely depressed, as in certain siluroids and in the frog-fish (*Lophius*).

The labial "tape" coalesces with the trabeculæ, and is continued on each side as a long cartilaginous *string*, which forms the pith of a tentacle which reaches as far as the end of the abdomen.

The branchial orifices are both open *right* and left (not the left only, as in the common kinds), and the fore limbs show their rudiments *outside* the opercular fold.

All the details of this, the flattest and most foliaceous of all chondrocrania described, are of the utmost interest, but cannot be described here.

In this type young toads with four large legs have no trace of a cartilaginous "columella;" and yet in the adult that structure is by far the largest I have yet seen, the "extrastapedial" itself being shaped like a waterlily-leaf, and is relatively of the size of the whole auditory ring of the bull-frog.

This species has only *one* vomer and no bony palatines; its original labial band forms a pair of nasal pouches, and it acquires *four more* pairs of these cartilages above and loses the lower pair.

*Dactylethra* has the upper element of the "girdle-bone" a "super-ethmoidal" plate; but the ossification of the chondrocranium itself is not in the ethmoidal but in the sphenoidal region. The huge tympano-Eustachian vaults open by one orifice in the pharynx; its "interhyal" is a ligament attached in the normal position; it has two true *tympanic bones* on each side (like those of certain birds), besides the large cartilaginous *annulus*, and its squamosal and quadrato-jugal are more like those of a tortoise than of an ordinary Batrachian.

Its quadrate bone is ossified, as in Ganoid and Teleostean fishes and tailed Amphibia.

But the Surinam toad (*Pipa monstrosa*) is a rarer creature than even *Dactylethra*, with which it agrees in being *tongueless*.

The embryo is wound like a tape round the large yolk-mass; it has a gaping broad mouth, with neither labial cartilages, nor horny jaws, nor "claspers." It has very small opercula, which do not cover the very early formed limbs: it has gill-arches and branchial vessels; but these are not branched, for there are no gill-tufts or processes that I can discover.

The cartilaginous skull of the embryonic *Pipa* is a very flat leafy structure, like that of the larval *Dactylethra*, but differing from it in many respects. At this stage the *fenestra ovalis* is forming, but there is neither stapes nor columella; at this time there is a large "cerato-hyal" in the usual place for a Batrachian larva, namely articulated to the mandibular pier not far above the condyle of the quadrate.

In ripe young *Pipæ* the metamorphosis is complete, although the *shape* of the adult skull is not attained. Ossification is already relatively nearly perfect; three pairs of labials now supplement the deficiencies of the nasal capsule, which is but little chondrified, and in the

auditory region the occipital arch and the two auditory capsules are one continuous tract of bone.

The stapes is perfect, and so is the columella with its two shaft-bones in each *stem*; its extrastapedial is like that of *Dactylethra*.

The mandible is perfect, the cerato-hyals *completely gone*, and the branchials are metamorphosed as completely (save that the "thyro-hyals" are not ossified) as in the adults of other Batrachia.

The frontals and parietals have already coalesced; in front there are nasals, preorbitals, and septo-maxillaries, a pair of each; but there is no vomer; there is a pair of styloid *palatine bones*.

The premaxillaries and maxillaries lie entirely on the under or palatine surface; there is no quadrato-jugal.

In the adult the bones are very coarse, fibrous, and with strong ridges and deep excavations, as in certain osseous fishes. There is no "girdle-bone;" the quadrate is now well ossified, and so is Meckel's cartilage, the "articulare" having grafted itself upon the rod.

In neither of these aglossal toads is there a "mento-Meckelian" bone formed at the symphysis.

In the adult *Pipa* the "occipito-otic" masses are stretched far out as large bony arms, on the end of which is the exquisite tympanic apparatus. Both in young and old the superoccipital region is well ossified over as a complete bony arch, and now, in the adult, the occipital condyles look *outwards*; the basioccipital region is a narrow synchondrosial tract.

These are some of the most noteworthy things in *Dactylethra* and in *Pipa*. The common toad shows most important differences from the common frog; but these aglossal types are rich in morphological variation and full of morphological meaning.

The satisfaction accruing to my own mind from the working out of these three (as well as other) types of the Batrachian skull will act as a strong stimulus to keep me a few years longer at the morphology of that group.

As the attachment of the mandibular arch to the skull is complex and very important, I venture to add a few remarks upon it.

*On the "Suspensorium" or Pier of the Mandibular Arch in the Amphibia generally.*

The Amphibia agree with three groups of fishes (namely, the "Marsipobranchii," the Chimæroids, and the "Dipnoi") in having their suspensorium confluent with the skull.

The simplest form of such a confluence has been shown in the present paper in the early condition of chondrocranium of the common toad, where the apex or dorsal end of the mandibular arch, *during chondrification*, unites with the outer side of the trabecular arch near its dorsal end. Afterwards, in the same type, this confluence is much more complex.

For a longer period in the Urodela the suspensorium is quite separate from the trabecula; as a rule it soon forms *three* attachments; but in this group, as in the Anura, it never unites *by confluence* with the next or hyoid arch.

Each of these groups has its typical method of attaching the suspensorium, and each has types that show remarkable modifications.

In *Menobrachius* and *Rana* (Huxley, *loc. cit.*) we have the two proper types of this structure in the adult.

In the former, the Sauro-batrachian, the apex of the mandibular arch unites with the trabecula near its apex on its outside by a process, the "pedicle," which lies beneath the trigeminal nerve.

A second or "ascending" process mounts over part of that nerve, especially arching over the orbito-nasal and the Vidian branch of the facial nerve, and it unites with the top of the *alisphenoidal crest* of the trabecula.

A third, the "otic process," grows upwards and backwards, and unites with the outside of the auditory capsule; it is pedate, and its thick end runs in front of the ampulla of the horizontal canal.

In the typical adult Batrachian suspensorium the primary union of the apex of the mandibular pier is afterwards lost, this part becoming mere fibrous tissue; but the lower part of the pedicle grows into a thick triangular process of cartilage with its base upwards, and this base becomes the "condyle of the pedicle;" it articulates with the side of the auditory capsule antero-inferiorly. This condyle has its counterpart in some of the Urodela as a swelling of the pedicle near the origin of the otic process below (Huxley, "On *Menobrachius*," plate 29. fig. 2).

In the adult frog the suspensorium is united by a gliding joint to the auditory capsule below, and by fusion of cartilage above and behind.

As far as my observations go, *Siredon* agrees with *Menobrachius*; in *Salamandra* the swelling answering to the "condyle of the pedicle" is very small, and the pedicle is suppressed. In the lowest type also, namely *Proteus anguinus*, the ascending process only is present, and the otic process is small. Some of the Batrachia differ from the frog in having the lower part of the "pedicle" greatly enlarged at first, but very small afterwards, forming a very small condyloid part; whilst the apex is not absorbed, but unites with the auditory capsule. This is seen in *Bufo vulgaris*.

Moreover in that type and in *Dactylethra*, when the legs are well developed, the otic process projects inwards *in front of* the auditory capsule. In *Pseudis paradoxa* this is very distinct as a thick, finger-shaped, free process, which passes inwards as far as the neck of the foremost ampulla.

The last is an instructive condition, as it partly breaks down the fence between the two groups of Amphibia; for in the Urodela the otic process is pedate, the *toe* projecting to nearly the same extent inwards as in *Pseudis*. The term "suspensorium" must not be applied to the part

which carries both the mandible and the hyoid arch in most fishes—sharks, rays, ganoids, and teleosteans.

This part, the “hyomandibular,” belongs to the second or hyoid arch, and has no representative in most of the Sauro-batrachia, nor in the Batrachia during their larval state.

In *Proteus*, however, contrary to what is seen in the other tailed forms, the proximal hyoid element is as massive as the mandibular pier, its immediate “serial homologue.” This “hyomandibular” of *Proteus* is attached by ligament to the suspensorium, the stapes, and the auditory capsule; it is not tilted upwards and forwards like its counterpart in the skate or osseous fish, but agrees with that of the shark in being directly articulated to the cerato-hyal. This, however, does not take place by direct superposition; but the hyomandibular is bevelled largely on its inner face, and overlaps the cerato-hyal. Had it been tilted upwards and forwards it would have applied itself to the outer face of the suspensorium in the manner of the flat fore end of the Batrachian “columella,” the *extrastapedial*.

Such a structure occurring in some low-generalized tailless amphibian could only be interpreted as the lump of organic clay out of which the columella had to be fashioned.

Every anomaly in a frog or toad that shows how thin the middle wall of partition is between the two groups will increase to me the probability that the hyomandibular of the *Proteus* is the Batrachian columella “writ large”\*.

*On signs of Vertebral Segmentation seen in the cephalic part of the Notochord.*

In my paper on the skull of the fowl (plate 82, fig. 3. *nc*) I have figured the notochord in the third stage as having *three* partially formed segments. The most distinct of these is the hindermost, and it is ossified. That osseous tract is the homologue of an *early* vertebral “centrum;” and if the other two spindle-shaped regions were to ossify separately there would be three rudimentary cranial centra.

In toads of the first summer (sixth stage of this paper) the shrinking notochord has become submoniliform, as in the chick, but it does not ossify.

In the Salamandrian Amphibia, however, the notochord acquires a bony sheath in front; and in *Seironota perspicillata* larvæ half an inch in length show *two* very well marked cranial centra, the front one with a perfect osseous sheath, whilst the hinder segment has bony grains scattered over the notochordal sheath. This last has the hourglass-shape, and corresponds accurately in form with the rudimentary centrum of the first cervical vertebra.

The dorsal ends of the trabeculæ occupy the apex of the notochord, and

\* It is *small* in *Spelerpes* and *Desmognathus*.

in these larvæ of *Seironota* the hinder half of the front notochordal segment is not invested by cartilage. But the hinder, feebly ossified segment has a cartilaginous plate on each side, which is already ossifying (as the ex-occipital), and these ossifying cartilages are seen to be the accurate counterparts of the "neurapophyses" of the first cervical vertebra.

Afterwards these cartilages grow forward and coalesce with the dorsal ends of the trabeculæ.

These facts are in perfect harmony with what I have been asserting for some years past, namely, that the basioccipital is not the hindermost centrum of a series of cranial vertebrae, but a single bone in the place of a series, the distinctness of which supposed series is lost, their segmentation being suppressed. The modified anterior end of the vertebral column forms the occipital arch. There are no developed cranial vertebrae in front of the "epencephalic," which used to figure as the hindermost of *four*.

### III. "Preliminary Observations on the Locomotor System of Medusæ." By G. J. ROMANES, M.A., F.L.S. Communicated by Prof. HUXLEY, Sec.R.S. Received November 1, 1875.

(Abstract.)

#### I. *Movements of the Medusæ.*

The movements of some of the Medusæ (e. g. *Sarsia*) appear to be as *voluntary* as are those of insects. Some of the discophorous species of naked-eyed Medusæ\*, when threatened with injury, manifest peculiar movements, which are quite distinct from the ordinary locomotor contractions. These movements consist in a very strong and protracted systole, followed by a slow and gradual diastole. This spasm-like series of movements is never performed by any Medusa except when the animal is being injured or threatened with injury.

#### II. *Fundamental Observations.*

§ 1. In the case of all the naked-eyed Medusæ which I have this year been able to procure (viz. thirteen species belonging to six of the most divergent genera) I find it to be true that excision of the extreme periphery of a nectocalyx is followed by immediate, total, and permanent paralysis of the entire organ. The severed margin, on the other hand, continues its rhythmical contractions as vigorously as when it was still *in situ*, and this for many hours after the operation. Among hundreds of observations I have only met with one exception to the otherwise uniform result of this operation. The exception occurred in an individual belonging to the species *Staurophora laciniata*.

\* I adhere to Forbes's classification only because I have not happened to meet with any individuals of the family Lucernariadæ.